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THE GENUS COLLINSIA. III. THE SIGNIFICANCE OF CHIASMATA FREQUENCIES AS A CYTOTAXONOMIC TOOL[1]

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The genus *Collinsia* Nutt. (Scrophulariaceae) includes twenty-one recognized species, divided into two groups (Newsom, 1929; Pennell, 1951). The species in one group have "sessile" flowers congested in whorls, with pedicels shorter than to no longer than the calyces of the lower whorls, and with flat, mature seeds. The species in the other group have pedicelled flowers, either solitary or in whorls, with the pedicels of the flowers of the lower whorls from as long as to longer than the calyces, and with either flat or thick, mature seeds. There are other differences between the species in these two groups but they are not as clear as those which have been mentioned. The basic chromosome number for the genus is 7; no polyploid species have yet been found (Garber, 1956, and unpubl.).

The species in each of the two groups apparently differ in their mean number of chiasmata per bivalent at metaphase I. With the exception of *C. corymbosa* Herder, the species with "sessile" flowers have mean values of 1.1–1.5 and the species with pedicelled flowers, 1.7–1.9 (Garber, 1956). *Collinsia corymbosa* was placed in the species group with "sessile" flowers by both Newsom (1929) and Pennell (1951), yet its combination of characters shows it to be somewhat intermediate between these two groups of species (Garber and Gorsic, 1956). The flowers are borne in dense, capitate whorls on pedicels 3–7 mm. long, with calyx lobes approximately 5 mm. long, and the mature seeds are thick. The mean number of chiasmata per bivalent at metaphase I in *C. corymbosa,* however, has been found to be 1.7–1.8, a value characteristic of the group of species with pedicelled flowers.

This paper presents evidence regarding the validity of chiasma frequency as a cytotaxonomic tool in studying relationships among species of *Collinsia* by considering the chromosome associations and aberrations

[1] This investigation was aided by grants from the National Science Foundation and the Dr. Wallace C. and Clara A. Abbott Memorial Fund of The University of Chicago.

in interspecific hybrids involving *C. heterophylla,* a species with "sessile" flowers.

Table 1. A comparison of certain morphological characters of *C. corymbosa, C. heterophylla,* and their interspecific hybrids (hcy 56632).

Character	Character *C. heterophylla*	Interspecific hybrid	*C. corymbosa*
Flower, position	"sessile"	*corymbosa*-like	"sessile"
Flower, upper lobes, length	prominent	intermediate	rudimentary
Flower, upper lobes, markings	present	present	absent
Flower, lateral lobes, color	blue-red	segregating*	cream white
Flower, tube color	pale blue-red	light blue	light blue
Flower, upper stamen filaments	basal spurs	no basal spurs	no basal spurs
Calyx lobes	glabrous	hairy, glandular	hairy, glandular
Leaf petiole	short	long	long

* Pale or light blue.

Materials and Methods

For the current studies, plants were grown from seed which was kindly supplied by Dr. R. Bacigalupi. Of the species involved, *C. corymbosa* is apparently restricted to the area around Fort Bragg, Mendocino County, California; *C. heterophylla* Buist, typical of the group with "sessile" flowers, may be found throughout the hilly portions of the western regions of California from the extreme south almost to the Oregon boundary; *C. sparsiflora* Fisch. and Mey., representative of the pedicelled group, occurs at low and middle elevations northward in the California coast ranges from Marin County and in the Sierra Nevada from Tuolumne County to Butte County.

Clusters of buds were fixed in a solution (6:3:2) of methanol, chloroform, and propionic acid (Pienaar, 1955), which proved superior to the familiar alcohol-acetic acid fixative, and the buds were then stored in a deep freezer until needed. Smears of pollen mother cells were stained with acetocarmine. Pollen grains were stained with basic fuchsin in lactophenol.

Hybridization Results

Interspecific hybridizations involving "sessile"-flowered *C. heterophylla* and *C. corymbosa* were easily accomplished. The yield and quality of the resulting seeds were excellent and approximately 90 per cent of the seeds germinated. Interspecific hybridizations involving the pedicelled-flowered species *C. sparsiflora* and *C. corymbosa,* however, were almost completely unsuccessful.

TABLE 2. Chromosome configurations at metaphase I in interspecific hybrids (hcy 56632) between *C. corymbosa* and *C. heterophylla*.

II	I	III	IV	Plant No. 3	5	6	10
7	....	....	....	14	48	42	19
6	2	....	....	19	15	61	18
5	4	....	....	12	4	24	18
4	6	....	....	2	....	4	4
3	8	....	....	....	....	2	....
5	1	1	....	1	2	....	1
4	3	1	....	....	....	1	....
3	5	1	....	1	....	1	....
5	....	....	1 chain	....	1	2	1
5	....	....	1 ring	....	....	....	1
4	2	....	1 chain	....	....	1	2
4	2	....	1 ring	....	1	....	1
3	4	....	1 chain	....	1	....	1
No. of pollen mother cells				49	72	138	66

MORPHOLOGICAL STUDIES. Only the interspecific hybrids between *C. heterophylla* and *C. corymbosa* were studied. The morphological differences between these species are so obvious that there is no difficulty in distinguishing these species. Certain characteristics of each species and their hybrids are summarized in Table 1.

In general, the interspecific hybrids resembled *C. corymbosa* in their vegetative characteristics, but the flowers were more like those of *C. heterophylla*. The hybrids were intermediate in height but almost as tall as *C. heterophylla*.

CYTOLOGY. The chromosome associations at metaphase I in the interspecific hybrids are summarized in Table 2. Most pollen mother cells had univalents and bivalents. A few pollen mother cells also had a trivalent or a quadrivalent. The mean number of chiasmata per bivalent at metaphase I in pollen mother cells with only bivalents was 1.3–1.4, which were the values observed for hybrids between *C. heterophylla* and *C. sparsiflora* (Garber and Gorsic, 1956).

No pollen mother cells had two trivalents or two quadrivalents. Since many pollen mother cells had univalents, it was conceivable that a ring of six chromosomes, the result of two reciprocal translocations involving one chromosome, could have been formed. Several configurations make this interpretation unlikely. The conclusion that at least a single heterozygous reciprocal translocation occurred in the interspecific hybrid appears to be reasonable. Pollen mother cells at telophase I often displayed a dicentric chromatid bridge and a very small fragment; a few cells had two bridges and two very small fragments (Table 3). These observations indicate that the interspecific hybrids had two heterozygous paracentric inversions.

TABLE 3. Number of pollen mother cells with dicentric chromatid bridges and fragments at telophase I in interspecific hybrids between *C. corymbosa* and *C. heterophylla*.

Plant No.	No. of bridges + fragments 0	1	2	No. of pollen mother cells
5	55	24	4	83
6	50	27	2	79
10	73	31	7	111

STERILITY. The interspecific hybrids were almost completely pollen-sterile, with less than 0.3 per cent stainable pollen grains. No seeds were set even when the flowers were hand-pollinated.

DISCUSSION

The group with "sessile" flowers includes the following species: *C. heterophylla, C. concolor, C. tinctoria, C. bartsiaefolia, C. multicolor, C. austromontana,* and *C. corymbosa* (Pennell, 1951). It has been possible to assemble data on the crossability, the fertility, and chromosome associations in interspecific hybrids involving *C. heterophylla, C. concolor, C. tinctoria,* and *C. bartsiaefolia* as well as in interspecific hybrids between *C. sparsiflora* and both *C. heterophylla* and *C. concolor* (Garber, unpub.; Garber and Gorsic, 1956; Hiorth, 1933).

When hybrids can be made between species, intragroup hybrids are more difficult to accomplish than intergroup hybrids, the yield of germinating seeds being much greater for the intergroup hybrids. Intragroup hybrids involving species with "sessile" flowers were fertile to some degree; intergroup hybrids were completely sterile. The hybrids between *C. corymbosa* and *C. heterophylla* behaved as intergroup hybrids.

Intragroup hybrids involving species with "sessile" flowers displayed only bivalents at metaphase I; intergroup hybrids had such chromosomal aberrations as heterozygous reciprocal translocations and heterozygous paracentric inversions. These chromosomal aberrations were responsible for the complete sterility of the intergroup hybrids. In this respect also, the hybrids involving *C. corymbosa* and *C. heterophylla* behaved as intergroup hybrids.

It seems reasonable to assume that barriers to hybridization have occurred for the species within the group with "sessile" flowers. Since such hybrids are fertile to some degree, such barriers would minimize the possibility of large scale introgression. The complete sterility of hybrids between species of different groups which easily hybridize serves as an effective barrier against introgression.

It is not yet clear what significance may be attached to the observation that hybrids between *C. corymbosa* and *C. heterophylla* have a mean number of chiasmata per bivalent at metaphase I of 1.3–1.4, a value also found in the interspecific hybrids involving *C. sparsiflora* and both *C.*

heterophylla and *C. concolor*. It is possible that this observation may be related to the length of the homologous segments in the chromosomes of the species in different groups.

Although the evidence may be interpreted to indicate that *C. corymbosa* does not belong with the species having "sessile" flowers, it appears more reasonable at this time to consider that *C. corymbosa* does not belong to the group of species including *C. heterophylla, C. concolor, C. tinctoria,* and *C. bartsiaefolia*. The other two species with "sessile" flowers, *C. multicolor* and *C. austromontana,* may yield critical information on this point. At any rate, the differences in the mean number of chiasmata per bivalent at metaphase I appear to have cytotaxonomic value in studying relationships among the species of *Collinsia*. It must remain for future investigation to determine the extent to which this tool may be used.

Summary

Interspecific hybridizations between *C. corymbosa* and *C. heterophylla* were easily accomplished, yielding a very high percentage of germinating seeds. The hybrids were completely sterile. Different numbers of bivalents and univalents were observed at metaphase I and, occasionally, a trivalent or quadrivalent was seen at the same stage. The multivalent was interpreted as a heterozygous reciprocal translocation. One or two dicentric chromatid bridges plus one or two very small fragments were observed at telophase I, indicating the presence of at least two heterozygous paracentric inversions. The combined data indicated that *C. corymbosa* does not belong with a number of species with "sessile" flowers but did not conclusively demonstrate that this species does not belong within the group of species having "sessile" flowers. The results indicate that differences in chiasma frequency appear to have cytotaxonomic value in studying relationships among the species of *Collinsia*.

The author is indebted to Mr. J. Gorsic for his technical assistance and to Dr. G. L. Stebbins for reading the manuscript.

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